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Review article

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The species problem evolving in the Anthropocene

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Abstract

The species problem dates to antiquity and encompasses three aspects since the modern synthesis: what species are, how they originate, and how they are delimited. Species are frequently thought of as evolutionary entities with real but fuzzy boundaries in space and time, but this concept struggles to constrain groups such as prokaryotes or lichens that push conventional notions of genealogy. Speciation is increasingly well understood, but questions remain regarding the origin, prevalence, and strength of reproductive isolation and genomic divergence of lineages. Delimitation is facilitated by sophisticated algorithms, but additional axes such as geography, ecology, and phenotype should be sampled, with speciation hypotheses tying those attributes to evolutionary processes. In this Review, we survey these topics, outline major open questions, and identify two new dimensions of the species problem: how these three dimensions are altered in the Anthropocene, and whether species have intrinsic value in themselves. Global change alters the intensity and trajectory of natural processes such as hybridization, and introduces new niches through urbanization and domestication, and new species are even being created in the laboratory. In the realm of conservation, it is unclear whether species stand apart from other facets of biodiversity in having a unique intrinsic value of their own.

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Key points

- The distinction between species as ontological individuals versus classes or kinds raises fundamental philosophical questions, including whether species are real or simply human constructs, and whether there is one universal or many different species concepts.
- A dichotomy exists between a genic view of speciation focused on genomic divergence and a biological view centred on reproductive isolation. Numerous examples exist for both, reinforcing the need for robust models of how species form and persist.
- Lineages can originate and vanish quickly, with only some persisting to move from incipient to completed species with stable boundaries; observed diversity can be a mixture of these processes, complicating efforts to understand speciation and delimit species.
- Although machine learning methods are advancing species delimitation, a key challenge is ensuring that observed differences correspond to hypothesized evolutionary processes and relevant speciation mechanisms.
- Human pressures are creating lineages with novel evolutionary trajectories and accelerating processes such as range shifts that increase hybridization and erode boundaries, each of which create difficulties for species delimitation while offering opportunities to study adaptation and speciation.
- The question of whether species possess intrinsic value distinct from their instrumental or relational roles, or from other dimensions of biodiversity, introduces a new ethical dimension to the species problem.

Introduction

The species problem — questions regarding the nature of species[1] — has been a central puzzle of biology since antiquity. Darwin evaluated this subject in detail, discussing conceptual frameworks that still resonate today[2]. Following the development of scientific species concepts during the modern synthesis[3], the species problem now encompasses three distinct dimensions[4]. First is what species are — in conceptual and philosophical terms[5] — and how they relate to what is observed in nature[6]. Second is how species arise[7] — the ecological, evolutionary, and genetic mechanisms of speciation. Third is how researchers delimit species[8] — what data, algorithms, and criteria reveal species boundaries[9]. These classically defined dimensions influence modern perceptions of species, and contribute to management and policy decisions guiding research and conservation efforts[10].

Philosophers and systematists converged in the 1970s[11,12] on the idea of species as ontological individuals. This idea contrasts with previous understandings of species as classes or kinds, categories into which organisms were sorted based on their traits. This complex philosophical distinction has subtle but crucial implications for research and conservation[10,13]. However, challenges arise not only from apparently common gene flow between species, but also from edge cases such as asexual, colonial, and multisymbiotic organisms, which can be difficult or impossible to understand as lineages or species[14,15].

Insights from genomics[16] and experiments[17] in the laboratory and the field increasingly clarify numerous dimensions of how species form and persist[18,19]. But investigations of reproductive isolation (RI) and hybridization raise fundamental questions about what mechanisms[20] regulate species boundaries[21]. Crucially, RI occupies a central place in understanding speciation[22], but explicit tests of how RI relates to the formation or maintenance of species boundaries are rarely incorporated into species delimitation (Box 1).

Increasingly sophisticated computational algorithms[23] and theoretical insights[24] now provide for robust, quantitative, and integrative analyses[25] across numerous axes of organismal variation[26] beyond simple genetic and phenotypic divergence. Researchers can increasingly quantify divergence in physiology, behaviour, ecology, and other dimensions in non-model systems, but it is often unclear how to link such differences to underlying speciation mechanisms[27]. Species delimitation requires not only the identification of lineages, but explicit quantitative testing of speciation hypotheses that tie patterns to processes, tying delimitation to speciation and species concepts.

Advances in the twenty-first century combining computation[24], genomics[16], and philosophy[28] have shed light on these three dimensions, but their interconnectedness[8,15] has not been reviewed in detail. Doing so here reveals two further new dimensions for the species problem, arising from the ongoing biodiversity crisis[29,30]. Ongoing global change in the Anthropocene[31] — expanding rapidly during the twentieth century[32] — increasingly places new pressures on species[33], promoting range shifts and other interactions that alter the tempo and mode of evolution[34]. These alterations offer enhanced mechanistic insights and engender a new field of Anthropocene speciation — the study of what processes and trajectories predominate in the twenty-first century and how they alter species boundaries and identities. Finally, the widespread imperilment of biodiversity and the attendant urgency of conservation[35] present complex questions regarding what dimensions of biodiversity are most valuable[36] and whether species themselves are special[30]. This concept links back to the first species problem — what species are[37] — influencing both empirical study[38] and conservation management[39].

In this Review, we synthesize developments across these five aspects of the species problem, summarizing conceptual and empirical progress and outlining major open questions (Fig. 1). We reflect on how the original three dimensions are transforming[29] during the Anthropocene, and discuss whether species have special moral and ethical value in conservation[30]. Finally, we provide guidance for future holistic and integrated approaches to studying and conserving species that consider the intricate interconnectedness of the species problem.

Species concepts

The ontology of species — the philosophical question of what kind of things species are (Fig. 2a) — is a complicated topic[1,40]. Prior to modern theories of evolution arising in the eighteenth and nineteenth centuries, species were often thought of typologically as classes or kinds defined by their properties. Species were viewed as organismal types to which specimens belonged based on their traits — for example, having wings or being red — which were thought to have arisen through special creation or some immutable fixity of nature, rather than via evolutionary processes.

In the 1970s, a view more congruent with evolutionary theory was outlined[11,12]. Under this view, taxa are unified not by their traits but by their common descent (Fig. 2b), and species therefore represent

Box 1 | Reproductive isolation

Reproductive isolation (RI) refers to the mechanisms that limit successful reproduction between individuals and reduce subsequent gene flow between populations and lineages, maintaining species boundaries and promoting diversification. RI is generally classified into two main categories[235]: prezygotic and postzygotic barriers. Prezygotic barriers[85] act before fertilization occurs, preventing mating or successful gamete formation. These barriers include temporal isolation (differences in breeding times), habitat isolation (different ecological niches), behavioural isolation (differences in mating signals or rituals), mechanical isolation (incompatibility of reproductive organs), and gametic isolation (incompatibility of gametes even if mating occurs). For example, in sympatric cichlid fish species in Africa's Lake Victoria, differences in male coloration drive female mate choice, reducing interbreeding despite coexistence[72].

By contrast, postzygotic barriers[89] act after fertilization has occurred. These barriers include hybrid inviability (hybrids fail to develop or die early), hybrid sterility (hybrids survive but cannot reproduce), and hybrid breakdown (hybrids might be viable and fertile initially but have reduced fitness in subsequent generations). For instance, crosses between different *Drosophila* species, or between horses (*Equus caballus*) and donkeys (*E. asinus*), usually result in sterile offspring[83]. Such barriers often result from Dobzhansky–Muller incompatibilities, where incompatible alleles reduce fitness[88].

The genetic signature of RI can manifest in a variety of ways, such as reduced introgression in hybrid zones and genomic islands of divergence that remain distinct despite high levels of gene flow across other parts of the genome[21,227]. This phenomenon is particularly evident when such regions are linked to factors such as mate choice, as observed in the hooded (*Corvus cornix*) and carrion (*C. corone*) crows[80]. Similar patterns are observed in sunflowers (*Helianthus*), where key loci associated with ecological adaptation resist gene flow, maintaining species distinctiveness despite high levels of ongoing hybridization[236].

For conservation, understanding RI helps in managing hybridization risks between native and introduced species[205] or parapatric congeners[203], which can affect the genetic composition of imperilled populations. Furthermore, identifying cryptic species that are reproductively isolated but morphologically similar is also vital for accurate biodiversity assessments and conservation planning[135].

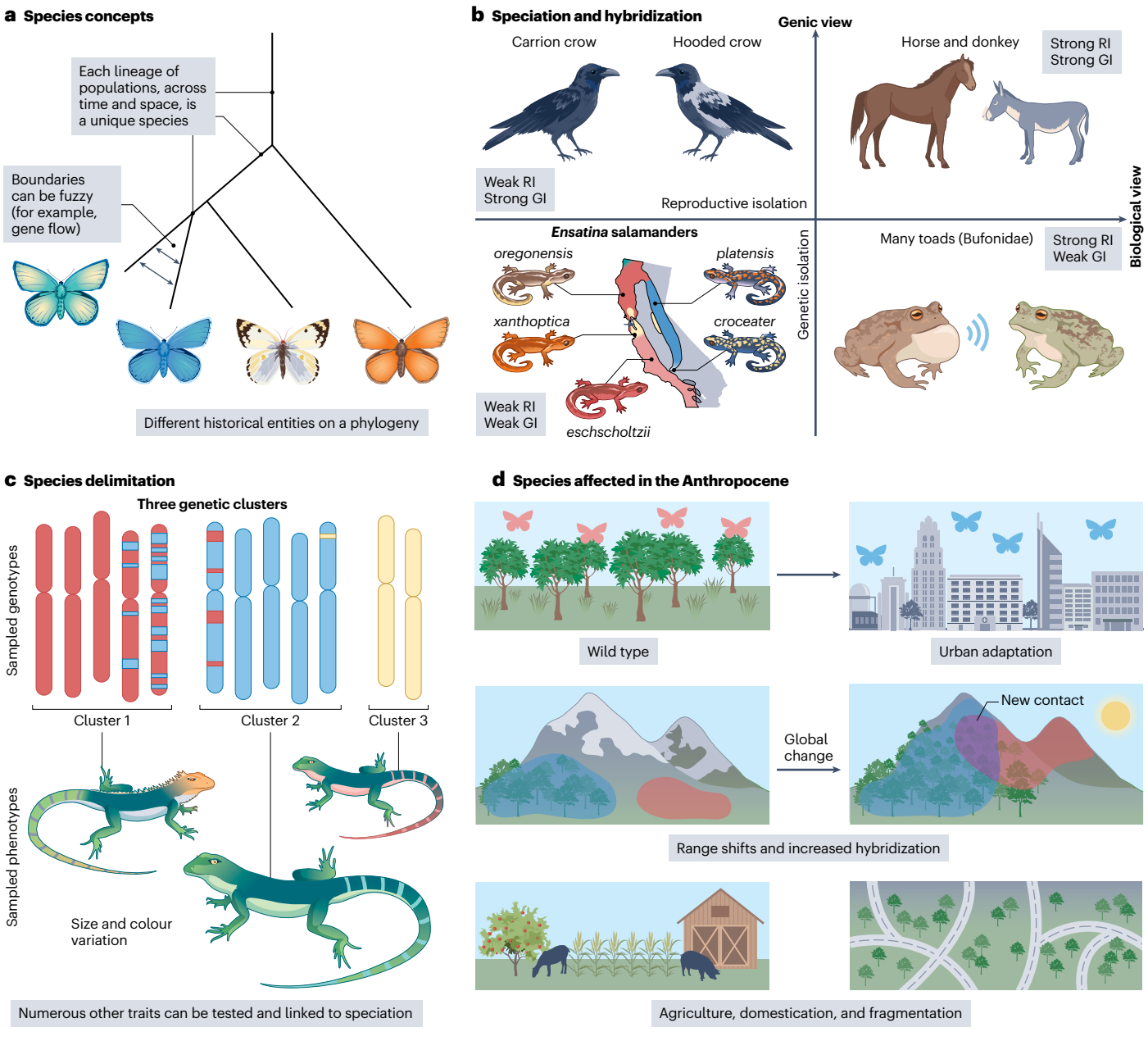
Overall, RI is often difficult to define, quantify, and compare across contexts and systems[235]. Greater attention should be paid not only to the generalized theoretical aspects of RI in evolutionary biology, but also to implementing empirical tests in species delimitation that examine the mechanisms and processes affecting reproductive success between individuals and gene flow between lineages.

"chunks of the genealogical nexus"[41] – distinct and unique segments of evolutionary history. Consequently, a species is an ontological individual (Fig. 2c), a historical entity in nature[42] that researchers define with reference to representative specimens diagnosed by taxonomists. Species are evolutionary lineages with beginnings and ends in space and time, all of which often have fuzzy boundaries[10] because of gene flow and the often-gradual nature of speciation and extinction[12]. Therefore, *Homo sapiens* are not defined simply by being warm-blooded hairless omnivorous bipeds with 23 pairs of chromosomes, but by their shared genealogical history with all individuals meeting that description, all of whom share those traits because of their common ancestry.

This view of species as individuals necessitates that species concepts be phylogenetic[43] – not any particular phylogenetic species concept per se[44], but deriving from and accurately representing evolutionary processes, which other concepts such as the biological species concept (BSC) often surprisingly do not[13]. A phylogenetic representation of lineages summarizes their evolutionary history, where speciation represents the boundary between tokogeny (genealogical interactions between individuals) and phylogeny (relationships between species with limited individual interactions[6]). Identifying this boundary is therefore one of the primary issues for both species concepts and speciation research.

But this simple definition of species as phylogenetic entities representing ontological individuals also has clear limitations[45] – edge cases and exceptions necessitate that investigators interrogate their concept of individuality (Fig. 2d). A huge fraction of life's diversity, including prokaryotes and many eukaryotic plants, animals, and fungi, does not reproduce sexually and therefore does not share this tokogeny versus phylogeny distinction. Many sexual eukaryotic species show some degree of introgressive hybridization[46], even across vast phylogenetic distances[47], with species boundaries that are often highly contentious owing to their fuzziness in space and time[48]. Taxa that are colonial[49], clonal[50], asexual[51], unisexual[52], or of questionable status as living organisms like viruses[53] might require multiple species concepts, rather than assuming a single universal species concept. Meta-organismal cases such as multisymbiotic lichens[54], bacterial biofilms[55], and coral holobionts[56] that resemble biological individuals strain definitions even further by including multiple distinct evolutionary lineages that interact in non-exclusive ways. Accordingly, some researchers suggest that many entities called species might be closer to classes than individuals even when taking evolutionary history into account[57].

Consequently, some workers question whether species are actually real things (species realism[58]), versus treating them more pragmatically[59] as human-imposed categories for segments of continuous natural variation[60] (anti-realism)[61]. Even assuming that species are real, another important question is whether there exists a single universal concept for species (monism), or many different possible concepts (pluralism) depending on the organismal, ecological, and evolutionary context[62]. Overall, greater integration of these concepts into empirical research is needed[10]. Researchers now frequently discuss operational species concepts in relevant contexts such as phylogenetics and taxonomy[63], but rarely offer overt consideration of realism, ontology, and theoretical concepts[48] in areas such as conservation management and species delimitation. Some authors have argued that realism and monism under the BSC based on RI often offer both pragmatic[38,64] and theoretical[37,65] advantages for conservation and delimitation. By contrast, other workers have pointed out that RI as a criterion is often incompatible with representing phylogeny[13] as well as underemphasizing geographic endemism of ecological and evolutionary distinct populations[66].



Speciation and hybridization

Speciation occurs via innumerable processes[7,67], although for asexual, prokaryotic, and other contentious taxa, speciation itself is often difficult to define[68]. For most sexual eukaryotes, the expected outcome is typically some form of RI[69], where speciation was historically thought to be marked by populations that rarely or never hybridize in nature[70] and subsequently accumulate Dobzhansky–Muller incompatibilities (Fig. 3a). Related to this process is the open question of whether RI and speciation occur more often via sorting of standing or ancestral genetic diversity versus novel adaptations — whether species are formed from new mutations and structural variants, or new combinations of old ones[20,71]. However, RI is not a necessary endpoint of speciation[72], merely

Fig. 1 | The five dimensions of the species problem. a, Species are ontological individuals representing a phylogenetic lineage of populations with fuzzy boundaries in space and time. They are not simply collections of traits sorted into categories; they are distinct (but not always discrete) historical entities connected by a phylogeny. **b**, Distinctiveness between species can occur along axes of reproductive isolation (RI; a biological view) or genetic differentiation (a genic view), depending on which mechanisms keep populations separated and the strength of this separation. Different taxa exemplify different combinations of these mechanisms. **c**, Discerning diagnostic differences between biologically meaningful clusters of populations is now routine, especially for the commonly investigated dimensions of genetics and phenotype. However, numerous other axes of variation are relevant to speciation, such as physiology, ecology, and behaviour, and should be investigated with mechanistic hypotheses linking them to speciation. **d**, Human-mediated global change can have an effect on natural processes, altering or eroding existing boundaries between species, and promoting new ecological and evolutionary trajectories. Outcomes can include Anthropocene speciation in urban environments, range shifts owing to climate change, new trajectories of agriculture and domestication, and impacts from habitat fragmentation. **e**, Biodiversity is widely held to have instrumental and relational value stemming from aspects such as ecosystem services and cultural identities, but these values can also apply to cells, populations, ecosystems, and even biomes. It is unclear whether species themselves have unique value. Furthermore, it is unclear whether species have unique intrinsic value in themselves, beyond their instrumental and relational values. These five interconnected topics are all crucial aspects of how people conceive of and study species, influencing both empirical research and applied conservation. GI, genetic isolation. Part **b** originally published in ref. 79 and adapted here with permission from the American Society of Ichthyologists and Herpetologists (ASIH).

an occasionally convenient marker thereof[13]. One way of interpreting this distinction is a fundamental dichotomy[73] between a biological view of speciation[74], which interprets gene flow as contrary to species independence; and a genic view[75], which regards genes as the primary units of differentiation.

In the former view, only lineages that are genetically isolated in nature qualify as species, but in the latter, species retain key attributes and evolve independently even as parts of the genome are homogenized by gene flow. These concepts can be visualized as a 2 × 2 contingency table with axes of RI versus genetic divergence, yielding four possible outcomes (Fig. 1b). Lineages with little genetic differentiation or RI are not species[76] — instead often classified as population structure[77,78], such as the ring species in *Ensatina* salamanders[79] — whereas species such as horses and donkeys with strong RI and genetic isolation are universally accepted. Taxa with little RI but strong genetic isolation linked to a few limited gene regions, such as those found between hooded and carrion crows[80], align to the genic view. Finally, there are many BSC-relevant taxa with strong RI in nature due to factors like behaviour, ecology, and phenology, such as toads (Bufonidae)[81], that lack strong intrinsic genetic isolation and hybridize readily in the laboratory. Consequently, there are several relevant areas for future investigation regarding the contribution of genic versus biological factors in initiating, promoting, and maintaining speciation.

A gap in understanding persists around the location, durability, and strength of RI[82,83]. Little is known about the order in which each type (prezygotic or postzygotic) evolves first or at all, and how often they interact[84]. Prezygotic RI can evolve quickly and often[85,86], involving both extrinsic factors such as habitat differentiation or flowering time, and intrinsic factors such as mate choice or incompatible genitals or gametes. Extrinsic prezygotic RI via temporal or sensory mechanisms can often be reversed by environmental changes that bring potential mates back into contact[87], but intrinsic mechanisms such as genital morphology are usually harder to undo[88]. For postzygotic isolation[83,89] — typically related to inviability or infertility of hybrids — mechanisms can also vary in their durability. For instance, hybrids can be less fit because they are ecologically maladapted[90] — which can change with environmental conditions — or because of genetic incompatibilities[91], which are unlikely to reverse. Additionally, little is known about the phylogenetic patterns of RI[68] across the speciation continuum[92] and the tree of life[93].

The second group of important questions centres on hybridization[94,95], which seems to be common[96,97] between diverging[78,98] and even distantly related species[47,99], resulting in a variety of outcomes (Fig. 3b,d). Hybridization can limit speciation through genetic swamping[100], promote speciation through increasing genetic diversity[101], and even cause speciation when two or more populations interact to create a new hybrid lineage[102] (Fig. 3c). However, the frequency and importance of these processes is unknown for most groups. Furthermore, adaptive, neutral, and deleterious introgression from hybridization[103,104] can occur after speciation is completed, with examples in both plants[105] and animals[106]. Investigating these dynamics is an important avenue to determine how post-speciation gene flow influences the trajectory of species' identities[107].

The third set of important topics involves the genetic mechanisms[20] affecting introgression and species boundaries[21]. The formation of genomic islands via selection against introgressed alleles at key loci allows for gene flow in some parts of the genome[108] while other regions remain distinct[109]. Consequently, species boundaries are often permeable[110], and semiporous genomes can even be favoured by selection[111,112]. A crucial but poorly understood aspect is the link between selection, phenotype, and RI, and whether the same loci are involved with all three[113,114]. At genomic scales, an important line of enquiry is the effect of recombination and structural variation on speciation[115,116]. The extent to which differences in genome structure such as structural variants, transposable elements[117,118], gene density, sex chromosomes, and recombination are related to variation in gene flow remains unknown[119]. Major hypotheses[120,121] include whether structural variants and transposable elements contribute directly to RI by modulating recombination and preserving locally adapted alleles, or have a more indirect role by influencing gene expression, chromatin accessibility, or epistatic interactions that affect hybrid fitness.

Species delimitation

The third major dimension of the species problem concerns how researchers recognize species in nature, or species delimitation[9,24]. These considerations encompass empirical issues of what data are necessary and sufficient to discover species[63], the theoretical criteria and algorithmic choices for making decisions at fuzzy boundaries[8] (Fig. 4a), and the push for integrative taxonomy[122] that considers process-based hypotheses for speciation mechanisms[123] (Fig. 4b) across organismal dimensions[124] (Fig. 4c) beyond genotype and phenotype[125] (Fig. 4d). Discovering biologically meaningful population clusters representing candidate species is now trivial, encompassing nearly any type of data using myriad computational approaches[24]. Going forward, the major challenges are now to quantify lineage distinctiveness more precisely under more specific evolutionary models[76,126] than before, and to link

these differences to testable scenarios regarding the processes that actually drove speciation[27,77]. These open questions break down along three important lines for future investigation.

First, very few methods — either statistical[9,127] or machine learning[24,128] — easily integrate other datasets beyond genotype[129,130]. But species can diverge along innumerable axes that are rarely

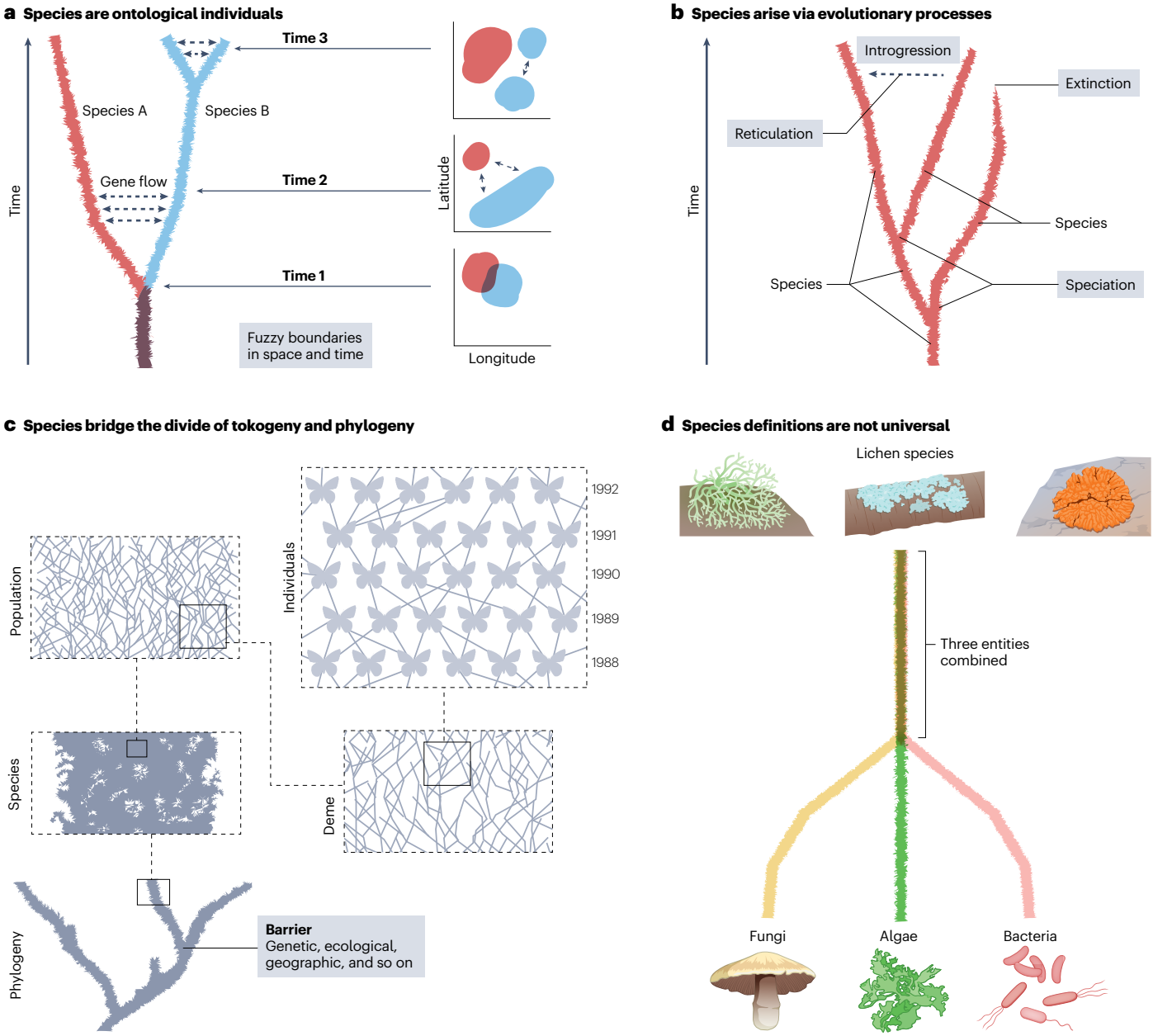


Fig. 2 | The nature of species. a, Species are now widely viewed as ontological individuals, phylogenetic lineages that are distinct evolutionary entities with real but fuzzy boundaries in space and time. That fuzziness arises from uncertainty over exactly where and when they begin and end, as well as genetic permeability of the species boundary to interspecific hybridization. **b**, Species arise via the evolutionary processes of speciation, reticulation, and extinction, which can each be represented graphically on a phylogenetic network. Crucially, each distinct branch on the phylogeny, including the internal branches, represents a species at a different point in time. **c**, For sexual species, speciation represents the boundary between tokogeny (genealogical interactions between individual organisms) and phylogeny (evolutionary relationships between species), typically associated with some form of isolation, whether behavioural, ecological, geographic, genetic, or otherwise. Consequently, species concepts must be phylogenetic in the sense of accounting for these boundaries and relationships, although this does not mean that any existing phylogenetic species concepts are necessarily correct or universal. **d**, Outside of sexual eukaryotes, numerous systems such as asexual prokaryotes, holobionts, and multisymbiotes strain species definitions based on individuality and phylogeny. For example, lichens behave as singular organisms but comprise up to three kingdoms of life and are typically classified primarily by their fungal component. The philosophical viewpoint of ontological individuality is congruent with evolutionary processes, but questions remain regarding its objectivity and equivalency. Part **c** adapted with permission from ref. 234, Maddison, D. R. & Maddison, W. P.

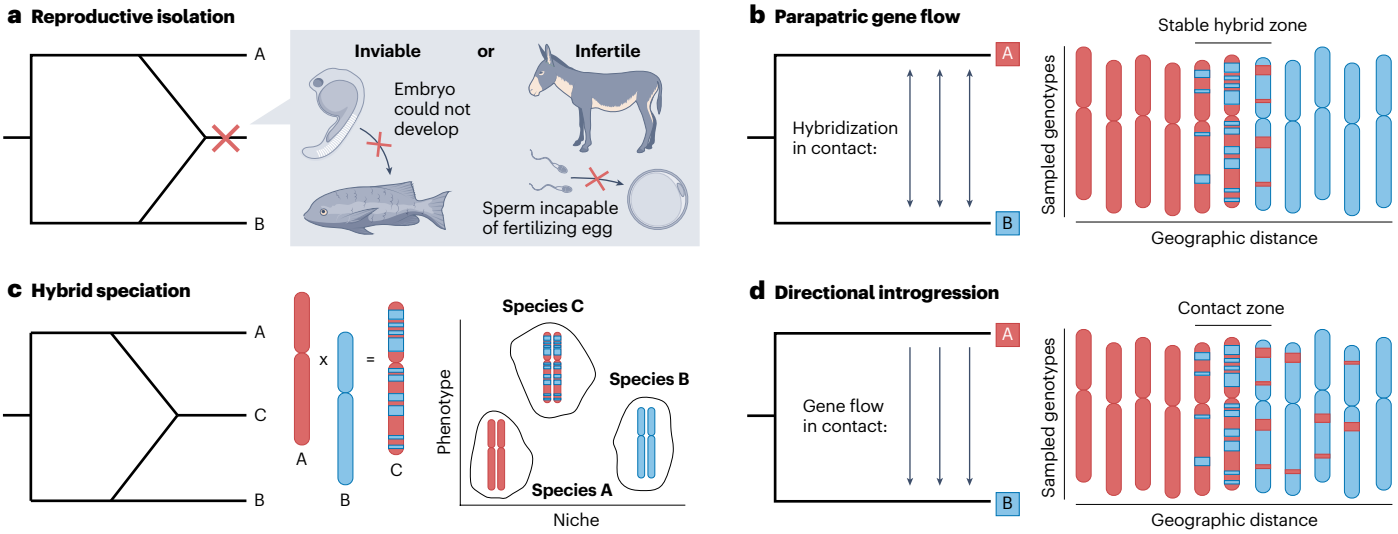


Fig. 3 | Speciation and hybridization. a, The most classic and complete outcome of speciation is strong intrinsic reproductive isolation (RI) that limits interspecific hybridization, typically via prezygotic mechanisms such as genital incompatibility, or postzygotic mechanisms such as hybrid infertility. These mechanisms are typically difficult to reverse, whereas other extrinsic mechanisms such as geographic isolation or ecological selection against hybrids can weaken under global change. **b**, When species do not have strong RI, interspecific hybridization might occur where they come into contact. If lineages are not isolated at all, they will typically fuse. If the two species are weakly isolated and have adaptive differences at one or more loci, stable hybrid zones can form in sympatry, particularly when geographic contact corresponds to environmental gradients. **c**, Occasionally, hybrid offspring can persist as a new, third, species-level lineage (species C). This can occur if the hybrids immediately have strong RI with their parents due to changes in ploidy or sexual system, or if they are more fit than either parent in a particular niche because of adaptive allele combinations or divergent phenotypes. **d**, If RI between two species is asymmetric, such as assortative mating in one (species B) but not the other (species A), directional introgression might occur, with alleles from one parental species introgressing into the other but not vice versa. Ultimately, speciation with gene flow and postspeciation hybridization seems to be common across the tree of life, requiring a variety of mechanisms to explain the maintenance of species boundaries and, in many cases, clarifying the underlying processes of divergence across the speciation continuum. Part **a** is adapted from ref. 91, CC BY 4.0 (https://creativecommons.org/licenses/by/4.0/).

considered in systematics, such as behaviour, physiology, and performance. Consequently, some questions regarding the origin and maintenance of species boundaries are difficult to answer with genetics alone, requiring phenotypic or other data to understand fully. Although some studies have examined diverse attributes in some species[131], there is ample room for incorporating a much wider range of organismal biology. A first challenge is simply to increase the number of data types, although only some of these will ultimately be related to speciation[132]. A subsequent major question is whether observed differences between lineages are actually involved in or represent a reasonable proxy for RI or other forms of genealogical independence[133]. Given the relative frequency of morphologically cryptic taxa[134], quantifying divergence in less conspicuous dimensions of the phenotype with strong effects on speciation and RI will often be particularly important[135].

Second, integrative species delimitation[124] should use varied datasets to distinguish between speciation and other processes that generate geographic genetic diversity[27]. Ephemeral lineages can arise within species[136] during a protracted speciation process[137] or through isolation-by-distance[138], generating locally adapted population structure[78] that is often detected by many common species-delimitation methods[139]. Determining thresholds in various summary statistics to distinguish between structure and species[76,77] is one way of approaching delimitation[22,123]. However, all such metrics can vary substantially across the genome, the tree of life, and the ecological and geographic context of speciation, and are affected by assumptions regarding selection and neutrality, and variation in RI mechanisms[140]. Therefore, using statistical thresholds as a proxy for speciation and RI might be telling researchers very little about underlying evolutionary processes, beyond indicating the existence, divergence, and stability of lineages through time.

Third, metrical cut-offs are only substitutes for the underlying ontological question — whether two lineages are independent in an evolutionary sense or interacting genetically as a single species[78]. The observation of significant differences in genotype or phenotype is therefore a primary hypothesis of speciation[76], to be tested[141] with a secondary hypothesis connected to the underlying processes[27]. Although difficult for most organisms, these subsequent tests must therefore link divergence across different axes of biological variation to the actual mechanisms responsible for lineage formation and persistence[77]. Consequently, the balance of evidence for the persistence of lineages despite homogenizing gene flow provides the most compelling rationale for their existence as species in an evolutionary context[10,140]. This framework represents the fullest expression of integrative taxonomy[124], including not only multiple data types to discover and delimit species[122], but also the mechanisms of speciation itself to explain their origin and persistence[27].

In practice, however, most species descriptions even in the twenty-first century are still based on a small number of specimens, typically with only cursory evaluation of major morphological differences and limited evaluation of genetic divergence from a few markers[142,143]. Many of these limitations are due to hard constraints on time, funding, and permitting. Genetic barcoding alone is often used for groups such as fungi[144], insects[145], and other invertebrates[146], applying somewhat

arbitrary thresholds, and edge cases such as lichens are typically classified primarily by their fungal component[54]. Given that the most diverse branches of the tree of life have only a fraction of their true diversity classified to any meaningful extent[147], pragmatic approaches to discovery[148] and delimitation[131] are likely to predominate for the foreseeable future. However, the framework described here provides a forward-looking guide to relevant philosophical and theoretical issues.

Species in the Anthropocene

Anthropogenic global change (including climate change, habitat alteration, and resource exploitation) has marked and rapidly increasing effects on the biosphere[33], modifying how investigators understand what species are, how they form, and how they are recognized[34]. Although these changes expanded substantially during the fifteenth and sixteenth centuries and intensified dramatically in the eighteenth through the twentieth[32,149], large-scale human impacts date back thousands or tens of thousands of years via hunting[150], domestication and agriculture[151], and habitat conversion by fire and forestry[152]. Anthropogenic forces can accelerate, reduce, or alter the course of nearly any ecological or evolutionary process[34], shifting the boundaries and identities of existing species. Humans are also creating new species in the laboratory[153], controversial efforts for de-extinction are underway[154], and a new set of species is evolving in human-associated niches[33]. Consequently, human-mediated effects seem to represent a novel, fourth dimension of the species problem, regarding how the first three dimensions described above are shifting in the Anthropocene.

One major example is anthropogenic impacts (Fig. 5a) that increase hybridization[155], such as range shifts due to global changes that bring lineages into contact[156]. Such human-induced introgression results in several major outcomes[157]. In some instances, this introgression contributes to erosion of genetic diversity[158], breakdown of reproductive barriers[155], and collapse of species boundaries[159] leading to extinction

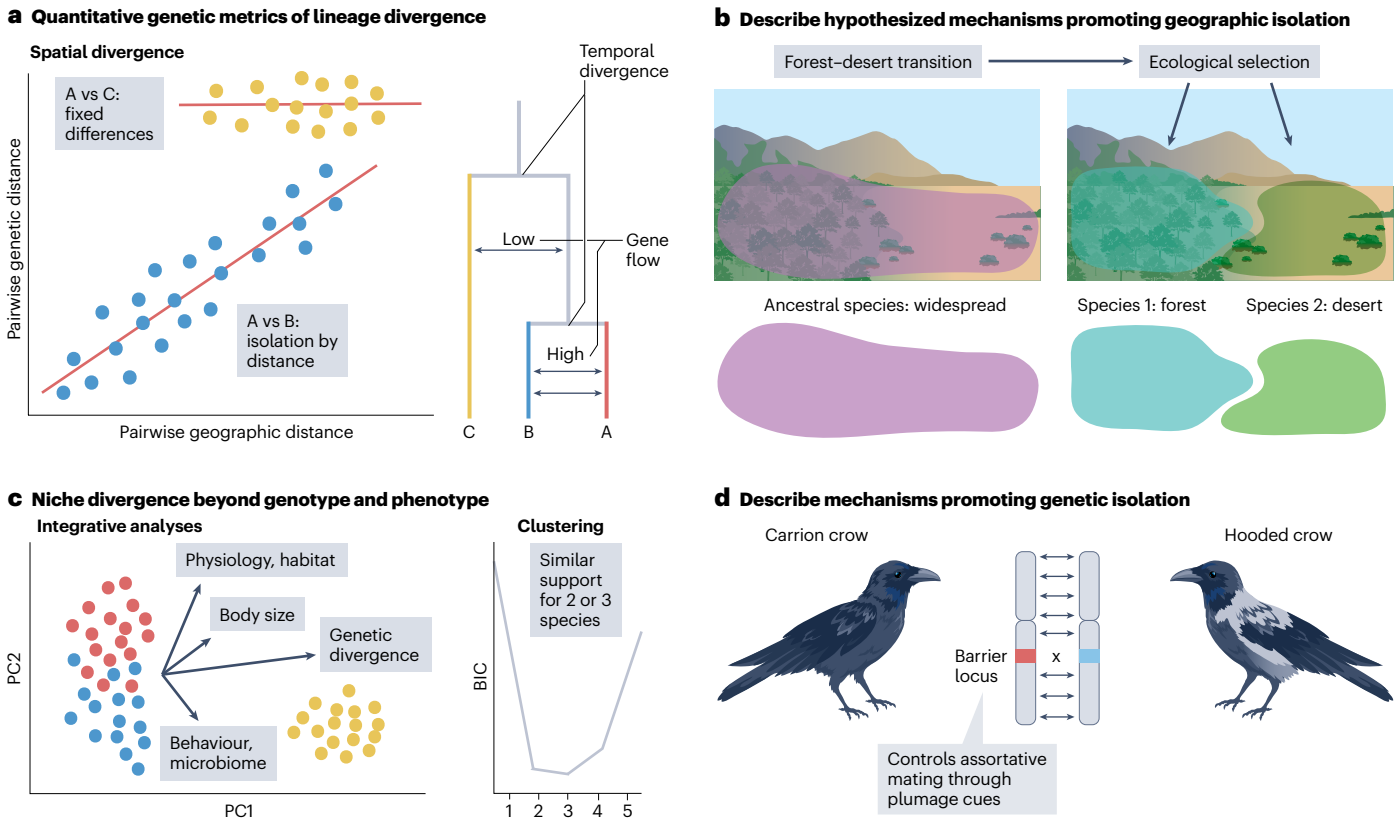


Fig. 4 | Species delimitation. a, Algorithmic methods for species delimitation often use quantitative metrics and thresholds but are typically limited to one or a few dimensions of genetic, geographic, or phenotypic divergence. For example, quantifying isolation-by-distance within and between lineages can identify non-spatial genetic discontinuities indicating fixed differences and a lack of gene flow between populations, but the next step must be testing specific evolutionary processes. Researchers increasingly use multiple computational approaches, but truly integrative species delimitation requires additional lines of evidence and hypothesized mechanisms to unify these combinations. **b**, One major component of species delimitation is testing mechanisms responsible for promoting geographic divergence and genetic isolation (such as range shifts or ecological selection) in the context of allopatric or parapatric taxa, either at present or historically in the case of secondary contact. **c**, Another major aspect of species delimitation is testing taxonomically underappreciated axes of organismal divergence beyond genotype and phenotype — such as performance, health, microbiology, physiology, and behaviour — which can have strong interactions with reproductive isolation and lineage diversification. **d**, Finally, additional emphasis is merited regarding the mechanisms responsible for genetic isolation, including locus-specific and genomic processes that promote, maintain, and reinforce species boundaries. These could include selection on adaptive alleles at functional loci, structural variants that limit recombination and preserve adaptive allele combinations, and transposable elements that modulate gene expression or affect hybrid fitness. As data sources and computational approaches become increasingly comprehensive, integrative species delimitation can incorporate more process and mechanism, so that resulting species are unified with both ontology and empiricism — described in a robust and coherent way as the end-products of evolution that incorporates their historical origins. BIC, Bayesian information criterion; PC, principal component.

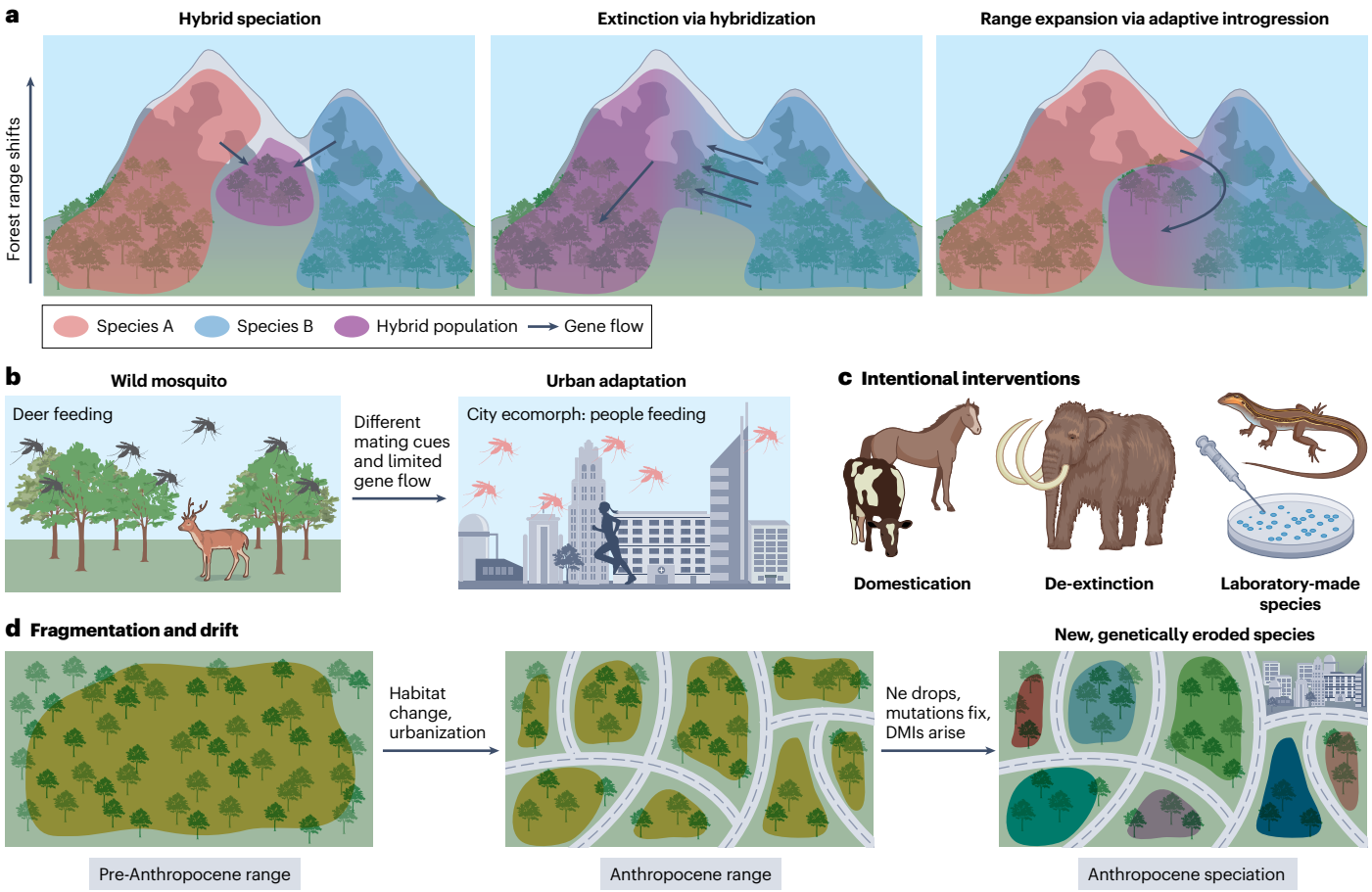


Fig. 5 | Anthropocene impacts. a, A major consequence of global change is altered habitats, climates, and ranges, leading many species into new environments and often into novel secondary contact with one another that would not otherwise have occurred. These ecological shifts can increase the rates of natural processes such as hybridization, leading to elevated frequency of hybrid speciation, extinction via genomic swamping, and range expansion via adaptive introgression. **b**, Another conspicuous outcome is human-associated divergence, such as urban evolution of species adapting to human habitats, potentially leading to Anthropocene speciation. **c**, Although limited in taxonomic scope, humans are also creating new species in the laboratory, domesticating and cultivating numerous plants and animals, and even controversially attempting de-extinction. **d**, Global change might even be altering the dominant processes of speciation, such as disrupting the role of prezygotic reproductive isolation and shifting emphasis away from divergent selection towards drift-based mechanisms resulting from fragmentation of ranges and decreased population sizes. Overall, species boundaries and speciation processes in the Anthropocene face a host of altered impacts, rates, and trajectories, leading to new, human-dominated assemblages of geographic genetic diversity. DMI, Dobzhansky–Muller incompatibility; Ne, effective population size.

via hybridization[160]. In other instances[161], it leads to increased genetic diversity[162] and enhanced fitness through the exchange of favourable alleles[163]. Additionally, there are now examples of anthropogenic hybrid speciation[164] — entirely new lineages with genomic content from multiple parents[165], potentially expressed as novel[166] or transgressive[167] phenotypes — resulting from human-induced contact and hybridization between parental species. Although the listed processes occur frequently in nature without anthropogenic influence[168], their increased speed and visibility in the Anthropocene represents a new combination of macroevolutionary pressures for many populations[162]. A potentially positive outcome is that these processes might be predictable and even controllable, perhaps facilitating hybrid genetic rescue as a strategy for conservation management[64].

Another conspicuous and informative scenario (Fig. 5b) occurs in the context of human-associated evolution[169], where novel selective pressures[170] cause rapid and quantifiable adaptive responses[171]. Numerous species are now human commensals[172] and have even begun to form new species in anthropogenic niches[173]. A famous example is the London Underground mosquito (*Culex pipiens f. molestus*), populations of which in urban environments such as subways have evolved genetic and behavioural isolation from wild-type varieties in several cities[174]. Another is the sweet vernal grass (*Anthoxanthum odoratum*), where populations at post-industrial sites in Wales are adapted to heavy metals in mine tailings and flower earlier, generating strong RI from the wild type[175]. Finally, domestication of myriad plants and animals (Fig. 5c) illustrates artificial selection leading to ecological and genetic divergence[151]. Anthropocene evolution consequently provides the opportunity to study adaptation and speciation in real time[176], with replicated experiments[177], comparison to historical mechanisms[178], and variation in ecological selection[179]. Lineages that are created, altered,

Box 2 | Ethics and values

In environmental ethics, the concepts of instrumental, intrinsic, and relational value[196] are fundamental but markedly different perspectives on the importance of biodiversity. Instrumental value refers to the utility of organisms, species, or ecosystems for human purposes. This value is conferred based on what nature can do for people — such as providing food, medicine, ecosystem services, or even just aesthetic beauty. For instance, pollinator conservation can be justified because of the role of those taxa in agriculture. However, if species are only valued instrumentally, they might be deemed replaceable or unimportant if alternative solutions are found. Relatively few species have irreplaceable instrumental value to humans, making it a limited tool to describe the full range of value in nature across millions of species.

Relational value focuses on the relationships between humans and nature, emphasizing values that arise from meaningful connections, responsible stewardship, and cultural identity. This perspective suggests that biodiversity can hold value because of the roles it has in these relationships, not just because of its utility (instrumental) or inherent worth (intrinsic). For example, ecosystems can have relational value due to their role in the cultural heritage and identity of local communities — both indigenous and national — in addition to their ecological or intrinsic worth. This historical and long-term relational importance would still exist even if future societies ceased to value it. Similarly, many species have relational values situating them between humanity and nature (for example, cultural icons such as bald eagles and pandas), but certainly not all — particularly those that are undiscovered or undescribed. Consequently, relational value alone is an insufficiently comprehensive explanation for the value of species in themselves and the necessity of their conservation.

Intrinsic value is that which species might have in themselves, independent of their utility or relationship to humans. The founding document of conservation biology[35] argued that species have intrinsic value due to their unique evolutionary histories. Other authors have invoked the aims or interests of species as intrinsically valuable or argued that their existence is subjectively but intrinsically valued by people. However, the validity of these claims is still debated[197]. Questions regarding whether species have unique and independent intrinsic value compared to other facets of biodiversity are crucial in the Anthropocene, where global change often threatens species' viability. If species do possess intrinsic value, it would provide a comprehensive explanation for why all species merit conservation, potentially justifying protection even when hybridization produces fitter individuals. Whether Anthropocene species would share this value is also an open question.

or eroded, by human-mediated mixtures of artificial and natural selection represent Anthropocene species[180] and provide opportunities to study these processes on accelerated timescales.

As novel genetic variation and phenotypic traits become established because of human activities[181], another question is how these mechanisms are shifting from pre-Anthropocene baselines. For instance, some data[156] suggest that habitat shifts driven by global change are affecting prezygotic barriers — such as ecological, geographic, or phenological isolation — more than postzygotic barriers such as genetic incompatibilities. Over time, the relative importance of prezygotic and postzygotic isolating mechanisms might therefore shift from previous expectations. One major outcome might be a change in the dominant mode of speciation in human-influenced populations[34,182], where divergence in alleles and phenotypes in the past stemmed more from selection, compared with fragmentation driving drift with cascading genetic incompatibilities in the future (Fig. 5d). Investigating human-induced shifts might also reveal how these processes change naturally through time. Rather than a single pre-human baseline, the Pleistocene, for example, was characterized by allopatric refugial dynamics during glacial cycles in many areas[183], whereas other periods and regions probably experienced very different pressures[184].

Finally, systematists are also faced with the challenge of delimiting and describing lineages that no longer have clear historical origins and fates on long-term ecological and evolutionary trajectories but are instead created or destroyed by human activities (accidentally or intentionally) within just a few years. Species delimitation must now contend with myriad anthropogenic effects on geographic genetic structure. Populations under taxonomic evaluation[185] might now have an anthropogenically influenced mixture of ancestries in addition to solely historically representative individuals[186]. One major pattern[187] is inbred or genetically eroded demes or human-affected subpopulations[188] that lack ancestral variation[189]. Another is populations with ancestry[190] from human-facilitated hybridization[191]. Furthermore, many extralimital populations from human-mediated migration[192] are now diverging in allopatry, while, alternatively, many lineages are slowly being swamped by extinction via human-facilitated translocation and hybridization[193]. Encouragingly, new algorithms using machine learning techniques[24] can include conservation-relevant data layers such as habitat encroachment and population trends to delimit human-modified population segments[129].

Species conservation

Global change is altering the conditions not only for speciation but for extinction as well, yielding a fifth dimension of the species problem centred on ethics: whether species themselves are especially valuable compared to other aspects of biodiversity. The founding document of conservation biology[35] stated: "Species have value in themselves, a value neither conferred nor revocable, but springing from a species' long evolutionary heritage and potential or even from the mere fact of its existence". But this is an assertion[194], not a fact[36], and is still debated[195] — biodiversity is valuable in numerous ways[196], but the species itself may or may not be a uniquely important axis[197]. Species have been argued to possess intrinsic value[198] (Box 2) — one that resides within species themselves — rather than instrumental or relational value deriving from the roles that they have in nature or their worth to people[196]. These arguments usually appeal to their unique and independent evolutionary heritage, ecological interactions, or even mere existence[197]. But similar arguments can also apply to genera, families, or even ecosystems[199] and have been made for numerous different facets of biodiversity with seemingly compelling support[200]. Consequently, there is still a question of whether species themselves have unique and independent intrinsic value that is distinct from other aspects of nature.

This question is not idle speculation. A conspicuous example is genetic swamping[201] leading to extinction via hybridization[193] in the red wolf (*Canis rufus*)[202], for which hybridization[203] with the coyote (*C. latrans*) is a primary threat to their survival and part of the basis for their legal protection[204]. But it is unclear that any individual red wolf is harmed by hybridization — hybrids in such cases can be more fit[205], particularly in the anthropogenically altered landscapes where this human-facilitated hybridization occurs. Only the existence and identity of *Canis rufus* as an ontological individual is affected. Consequently, the question of what, if any, unique, independent, or special intrinsic value is possessed by the red wolf, and whether this value, if it exists, merits exceptional attention or protection compared with that of the novel hybrids, is crucial. This question arises because protecting individual red wolves is not necessarily the same, in theory or in practice, as protecting the red wolf as a species. For instance, culling or sterilization (of, in this case, coyotes or hybrids) is often used to protect many taxa, a controversial practice[206] that prioritizes species and population health over the lives of individual animals, even those that are native to ecosystems[207].

Given the effect that such questions of value can have, an ethically comprehensive framework is therefore needed to evaluate claims about the nature of species and, in turn, their value relative to other facets of biodiversity. Since the 1980s, biodiversity's value has been examined extensively, with a variety of both compelling rationales[208] and troublesome implications[209]. At least three arguments for the intrinsic value of species[210] have been widely described and defended in the environmental ethics literature[198], with various strengths and weaknesses.

One key argument is based on the potential interests of species as ontological individuals. The lives of individual organisms, from bacteria to humans, each have intrinsic value, because each has interests — to live, flourish, and reproduce[211]. As species are also individuals (groups of living things as an ongoing process[212] with interests of their own), perhaps they share this value[30].

Crucially, the interests of species do not always align with their individual members, exemplified in the case of culling, suggesting that their intrinsic value might be unique and independent. But strong objections[213] have been raised to this view[214,215]. For example, one might question whether a species is really a living thing in the necessary sense, given that the health and interests of a species are more abstract concepts than concrete realities. Similarly, species do not have minds or mental states — they cannot perceive or act in their own interests as a collective. If a species is harmed, no sentient being experiences that harm — any suffering reduces to that of individual members of that species being harmed, whose interests are already accounted for based on the intrinsic value of their individual lives. Consequently, one might question whether conation is necessary for an individual living thing to have intrinsic value[209], something a species lacks.

A second argument is that species have valuer-dependent intrinsic value, derived from humans valuing species solely for their unique existence, not just what they can do[198]. This framework is often expressed in legal policy[210]. In some senses, it is uncontroversial — it becomes true simply by believing it. But objections include whether this value is durable or intrinsic if it depends on human valuers, and again, whether it is uniquely ascribed to species versus other evolutionary lineages or ecological collectives such as ecosystems or biomes. Value that depends on someone being around to confer it might instead simply be instrumental — as a means to an end of satisfying some aesthetic, spiritual, or moral preference of humankind.

A third more philosophically abstract view holds that species have objective intrinsic value — a universal quality that exists regardless of context or observation[194]. This value is unique and independent because of species' evolutionary trajectories and historical origins — each species is a distinct form of life derived from generative evolutionary processes[200]. Every such entity in nature represents an individual set of evolved and adapted characteristics — irreplaceable designs[194] — comprising the irrevocable intrinsic value mentioned previously[35]. But objections[210] include whether truly objective intrinsic value can exist at all — for example, religious arguments invoking a higher power are common in human belief systems, but empirical cases for such value are far more difficult and perhaps impossible to ascertain. Another objection is that such value would either have to vary as evolutionary distinctness changes through time and space (meaning that some species would be more valuable than others, a contentious proposition that has nonetheless been made[195]), or it would have to be trivially assigned to nearly all facets of the evolutionary process, not just unique and independent species.

Belief that species have intrinsic value is widespread and durable[197]. By contrast, arguments for a unique and independent source of this value[200] — distinct from their instrumental or relational value and broader intrinsic values that are shared with other aspects of the biosphere[196] — are incomplete and controversial[210]. Limited cases have been made that are congruent with species as ontological individuals which arise via evolutionary processes — because such individuals have interests, are valued by humans for themselves, or represent irreplaceable designs in nature — and other arguments might be possible. But intrinsic value might also not be necessary for effective conservation management in a practical or conceptual sense[216], compared to a more comprehensive approach to preserving nature[217]. Both policy and management can be conducted[218] based on protected areas, ecosystems, communities, populations, and individuals, with minimal reliance on notions of species themselves[219]. Given the emphasis placed on species in policy and the centrality of species as units of analysis[220] in ecology, evolution, and conservation[221], more scholarship is merited on this question and its potential implications, including whether such values extend to Anthropocene species.

Summary and future directions

In the twenty-first century, substantial progress has been made on the species problem[4]. Regarding the question of what species are, philosophers now have a robust and coherent definition of ontological individuals — spatiotemporally bounded evolutionary lineages — yielding a phylogenetic concept of species unified by genealogical descent[11,12]. In terms of speciation, investigators now have a profusion of data and models describing myriad mechanisms that initiate lineage formation and persistence[7,67]. For species delimitation[9,24], increasingly detailed datasets and sophisticated algorithms now permit integrative, multidimensional analyses to identify population clusters across numerous axes of variation[129] and link these to evolutionary mechanisms and speciation hypotheses[24]. But there are still crucial open questions stemming from these three dimensions — along with two new ones — for which future research will have potentially transformative effects across disciplines dealing with species.

First, the question of what species are has not been settled in terms of reality and concept. Anti-realism[61] — the idea that species do not have an independent, objective existence in nature but are instead human constructs to classify variation in biodiversity[58] — retains currency with many philosophers[194]. Even if one subscribes to realism, the question

Glossary

Anthropocene
A broadly defined term, taken here to begin no later than the European Age of Exploration in the fifteenth and sixteenth centuries and expanding rapidly during the Great Acceleration in the mid-twentieth century.

Anti-realism
Anti-realism argues that species are human-constructed categories without inherent or objective reality.

Classes or kinds
Sets of entities defined solely by traits or features that they possess intrinsically, without the need for any historical continuity between individuals.

Conation
Aspects of behaviour associated with purposeful action, willpower, and the drive to achieve goals, reflecting the intentional and volitional component of decision making.

Deme
A locally interbreeding subpopulation within a species, typically characterized by limited gene flow with other such groups across generations and elevated average relatedness among its members.

Dobzhansky–Muller incompatibility
A genetic mechanism in which interactions between independently evolved alleles at two or more loci in hybrids lead to reduced hybrid fitness.

Ephemeral lineages
Lineages emerging from a rapid and often short-lived process in which new species arise quickly but might not persist, which can occur often during protracted speciation.

Genetic rescue
The process of increasing genetic diversity and hopefully fitness of small or inbred populations by introducing genetically distinct individuals, reducing inbreeding depression and enhancing viability.

Genomic islands
Regions of the genome that show high genetic differentiation between species or populations despite overall gene flow, arising from numerous mechanisms such as selection or variable recombination.

Hybridization
Genetic exchange between individuals of two species.

Introgression
The process of hybridization and backcrossing that introduces alleles from one species to another.

Monism
Monism suggests that a single universal concept defines and classifies all species.

Ontological individual
A phylogenetic entity persisting through space and time as a cohesive, evolving unit, despite fuzzy boundaries due to gene flow, extinction, or speciation.

Protracted speciation
A slow, gradual process in which genetic divergence and reproductive isolation accumulate over time, leading to more stable and enduring species with longer intermediate stages.

Pluralism
Pluralism argues for multiple, equally valid species concepts, reflecting the complexity of biological diversity.

Realism
The view that species are real, objective entities that exist independently of human classification.

Reproductive isolation
A term that encompasses a wide variety of mechanisms and measurements, expressed most generally as the effect that population-level differences have on gene flow.

Structural variants
Larger (usually >50 bp) genomic alterations such as deletions, duplications, insertions, inversions, and translocations that affect genome structure and function.

Tokogeny
The genealogical or other biological relationships between parent and offspring or other ancestors and descendants, applied to individual organisms rather than species.

Transposable elements
Repetitive DNA sequences capable of moving within a genome via cut-and-paste or copy-and-paste mechanisms, forming a major component of eukaryotic genomes, often promoting structural and regulatory variation.

of monism versus pluralism — whether there is one species concept or many — has both empirical and philosophical relevance considering cases such as microorganisms, holobionts, and multisymbiotes.

Second, the increasing prevalence of genome-scale data[19] and sophisticated evolutionary theory has clarified numerous dimensions of the speciation process[222], but several increasingly complex[223] yet fundamental questions[20] arise from these data[224]. The first is when, where, and how prezygotic and postzygotic RI form, contribute to speciation, and interact with other ecological and geographic mechanisms[82]. The second is understanding the effects of hybridization before[225], during[226], and after[47] speciation. The third is what part is played by genomic attributes such as islands of divergence[227], coldspots and hotspots of recombination[228], structural variants[116], and transposable elements[118], and via what mechanisms[115] — understanding how genome structure[229] and function[228] contribute to species boundaries. Linking these together can answer how standing ancestral diversity[71], new mutations[230], and introgressive hybridization[102] interact to facilitate speciation.

Third, the conceptual and methodological sophistication of new approaches to integrative species delimitation[24] raises two major considerations for future research. First is the need to gather data along additional dimensions of organismal biology, which can be incorporated using increasingly sophisticated machine learning algorithms[129]. Many crucially relevant axes of variation — such as behaviour, performance, and physiology — have rarely been considered in species delimitation. Additionally, beyond simply identifying diagnostic differences[76], researchers must further develop mechanistic expectations for when and why species will vary in diagnostic attributes, linking evolutionary mechanisms to speciation hypotheses[27]. Consequently, scientists can now attempt to understand the relationship between the concept of evolutionary lineages, mechanisms of genetic and phenotypic differentiation, and markers of evolutionary independence such as RI, genomic divergence, and diagnostic traits. Such a synthesis can thereby account for the evolutionary basis of species as ontological individuals, the mechanisms and process of speciation, and integrative species delimitation. Stemming from this synthesis of the three historical dimensions of the species problem are two new empirical and philosophical dimensions with numerous open questions.

Fourth, human-induced global change in the Anthropocene is not only accelerating ordinary ecological and evolutionary processes[34] but introducing its own unique effects on selection and adaptation[231]. Global change alters evolutionary dynamics at numerous scales[232], and

urban evolution, laboratory protocols, and de-extinction efforts are even leading to the formation of new species created by, associated with, or dependent on humans[172]. These dynamics yield at least three important questions for Anthropocene speciation. The first is in what ways natural (or at least pre-Anthropocene) speciation and extinction dynamics shift as populations respond to mixtures of artificial and natural selection[164,233]. The second involves how species boundaries are erected, eroded, or modified under global change[173,182]. The third is how researchers can delimit species when taxa can contain heterogeneous assemblages of anthropogenic and natural gene pools[24,129]. Understanding these dynamics will not only give insight into ecology and evolution in real time but also illuminate relevant dimensions of conservation management and sustainability into the future.

Fifth, the Anthropocene biodiversity crisis helped to birth environmental ethics[208] — the moral philosophy of nature's value. But one foundational claim in conservational biology lacks an equivalently strong philosophical basis — whether species themselves are intrinsically valuable. That species have instrumental and relational value for their roles in ecosystems and contributions to people is not controversial[196], but whether they have value in themselves alone has yet to be established. If so, it is also unclear whether this value resides in the identity of the species itself or only the individuals of that species, and whether it is unique and distinct from the value of higher taxa or other facets of biodiversity. There are several claims[210] that species are intrinsically valuable based on their interests for flourishing, their appreciation by people, and their unique histories and irreplaceable designs. However, these arguments have compelling objections and veer into murky moral assumptions and thorny ethical implications. Greater interrogation of the potential intrinsic values of species has the potential to ethically harmonize conceptual and empirical approaches to basic research in ecology and evolution at the applied interface with conservation, management, and policy.

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